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AGE AND LENGTH AT WEANING AND DEVELOPMENT OF DIET OF PANTROPICAL SPOTTED DOLPHINS, *STENELLA ATTENUATA*, FROM THE EASTERN TROPICAL PACIFIC

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ABSTRACT

Using stomach contents from 203 spotted dolphins (*Stenella attenuata*) killed in the yellowfin tuna fishery, we modeled the weaning process of calves. Spotted dolphins began to take solid food at approximately 6 mo of age, or 115 cm, but continued to suckle until they were nearly 2 yr old. Calves tended to feed more frequently on squid as they got older, which suggested there was a shift in diet during weaning. The average age and total body length at weaning was estimated to be 0.8 yr (approximately 9 mo) and 122 cm. The oldest suckling calf was almost 2 yr old, which suggests that some calves continued to suckle for more than a year after they could have been weaned. A better understanding of the weaning process, especially quantifying the period of time when calves are nutritionally dependent on their mothers may lead to a better evaluation of their potential vulnerability to the disturbance caused by the yellowfin tuna purse-seine fishery.

Key words: wean, stomach contents, calf, spotted dolphin, *Stenella attenuata*, diet.

The diet of spotted dolphins, *Stenella attenuata*, in the eastern tropical Pacific (ETP) has been well documented (Perrin *et al*. 1976, Bernard and Hohn 1989, Robertson and Chivers 1997, Galván Magaña 1999). Although juveniles and adults eat essentially the same prey, little is known about the weaning process, prey choice, or nutritional requirements of juvenile dolphins from birth to independence. The nutritional requirements of young mammals are significantly different than those of adults (Nicolson 1982), because they require a higher relative caloric intake to fuel their rapid growth, especially in the first few years (Blaxter 1961). This is expected to be reflected by an increase either in the relative volume, feeding frequency, or caloric content of the prey consumed.

A better understanding of the transition to nutritional independence is necessary to evaluate the impact of tuna purse-seine fishing on dolphins (Gerrodette 2002). During fishing on dolphins the purse-seine chase begins once a school of dolphins "carrying" sufficient tuna is detected, either by boat or helicopter. Speedboats are sent ahead of the large seiner to help slow and concentrate the dolphins so the net can be set around them. As the chase proceeds, the once homogeneous school tends to break up into smaller subschools in an apparent effort to avoid capture. Once the dolphins have been slowed and the school has been concentrated, the net is drawn around the school, while the speedboats patrol the opening to keep dolphins from escaping and taking tuna with them. The net is then "pursed" to trap the tuna swimming below the dolphins, after which the fishermen perform the "backdown" procedure to release the dolphins at the surface. Most are released, but some may become entangled under sections of collapsing net or suffocate while trying to surface from below the net (Coe *et al*. 1982).

As reported in Archer *et al*. (2001), there is evidence that some nursing calves are separated from their mothers during purse-seining. The degree to which this separation leads to unobserved mortality is a factor of the length at which calves may be considered independent of their mothers. Although weaning is not necessarily equivalent to full independence, especially in highly social animals, it can be used to estimate the age below which calves have a lower probability of survival if orphaned (Nicolson 1982).

In this paper, we model the weaning process using a larger sample of stomachs collected from pantropical spotted dolphins in the ETP for which length and an estimated age were also known. We examine and discuss several potential biases in our model, including the effects of purse-seine chase duration on stomach content sampling. We also describe the changes in prey composition and prey size as calves grow.

Methods

Robertson and Chivers (1997) previously examined the food habits of spotted dolphins (*Stenella attenuata*) from the eastern tropical Pacific (ETP). For this study we selected all specimens that they examined that were less than 180 cm long and had food or milk in their stomachs (n = 203). These dolphins were collected between 1989 and 1991 by biological technicians placed aboard US tuna purse-seine vessels fishing in the ETP (Fig. 1). Stomachs were frozen on board the vessel and stored frozen in 0° in the lab until examination.

Stomachs were examined and prey quantified according to the methods in Robertson and Chivers (1997). Milk was noted as present when an oily, yellow-white liquid was found. Fish otoliths and squid mandibles (beaks) were identified to the lowest possible taxon using voucher collections (Los Angeles County Museum of Natural History and Santa Barbara Museum of Natural History) and published identification keys (Fitch and Brownell 1968, Fitch 1969, Butler 1979, Wolff 1982, Clarke 1986*a*). Those otoliths and beaks showing little to no deterioration from digestion were measured (Robertson and Chivers 1997), and prey size was determined using appropriate regression equations (Wolff 1982; Clarke 1986*a*; SWFSC, unpublished data).

We examined the relationship between the stomach fullness index (SFI, Robertson and Chivers 1997), a dimensionless measure of the weight of the forestomach contents relative to the initial weight of the forestomach, and the duration of the chase to see if this factor affected the volume of stomach contents (*i.e.*, led to regurgitation). Length of chase was defined as the amount of time

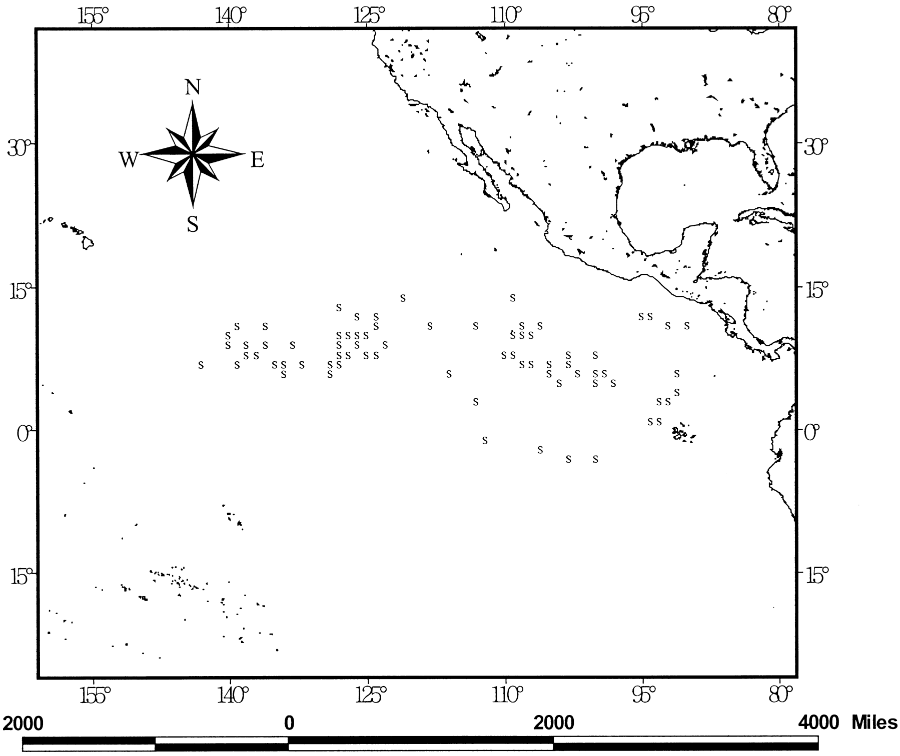

Figure 1. Distribution of 80 purse seine sets in the eastern tropical Pacific from which 203 specimens used in this study were collected.

elapsed between when speedboats deployed from the purse-seiner entered the water and the net was released, binned into 15-min intervals. Robertson and Chivers (1997) showed that animals killed earlier in the day were more likely to have food in their stomachs, a result of nighttime feeding. To correct for this effect, we used the hour that the chase started, binned into 3-h intervals, as a covariate in the analysis of SFI relative to duration of chase.

The age of 29 specimens was estimated from tooth decalcification and thin-sectioning.[1] Growth layer groups (GLGs) were measured from an image of the tooth captured and read using a Data Translation QuickCapture™ frame grabber. GLGs were measured to the nearest micrometer three times by the second author (KMR). Greater than 90% of the three serial readings were within 0.25 μm of each other. Partial or incomplete GLGs were measured and an age estimated by taking the partial GLG measurement and dividing it by the average width of the GLG at that given age (Myrick *et al.* 1984). Because one GLG was assumed to correspond to

[1] Myrick, Jr., A. C., A. A. Hohn, P. A. Sloan, M. Kimura and D. D. Stanley. 1983. Estimating age of spotted and spinner dolphins (*Stenella attenuata* and *Stenella longirostris*) from teeth. National Oceanographic and Atmospheric Administration Technical Memorandum NMFS-SWFSC-30 (unpublished). 17 pp. Available from SWFSC, 8604 La Jolla Shores Dr., La Jolla, CA 92038.

one year of growth, fractions thereof are assumed to represent an equivalent fraction of a year.

To model weaning, we used a standard logistic equation,

$$p = \frac{1}{1 + e^{-a-bx}},$$

where x is either length or age, and a and b are the fitted parameters of the model. Models for the probability of milk, *p(milk)*, or food, *p(food)*, were fit separately. For each specimen, p was recorded as 0 if milk or food was absent in a stomach or 1 if present. Parameters were estimated by minimization of the negative logistic log-likelihood function (Allison 1999),

$$-\log L = -\sum_i p_i(a + bx_i) + \sum_i \log(1 + e^{a+bx_i}).$$

To estimate 95% confidence intervals, 5,000 bootstrap replicates were conducted. For each replicate, the model coefficients were estimated. With these coefficients, p was calculated for 100 evenly spaced points between the minimum and maximum values of x present in the original data. The lower and upper 95th percentiles of the estimates of p were collected for each x. Logistic curves representing the 95% CI's were then fit to these data.

The length at which *p(milk)* = 0.01 was chosen as the upper bound for "weaning" animals, as this marks the point where a very small fraction of animals (1%) would be expected to still be nursing. In order to make sample sizes as equal as possible, the median length below this value of all individuals with solid food in their stomachs was used to split specimens into "small-" and "large-" weaning calves. We examined differences in the number, frequencies, and size of prey taken between the two groups. Fish and squid were treated separately, and the most commonly occurring families of each (fish: Myctophidae; squid: Ommastrephidae, Onychoteuthidae, Enoploteuthidae, Mastigoteuthidae, and Cranchiidae; Robertson and Chivers 1997) were also examined.

We also used a *k*-means cluster analysis (Wilkinson 1997) to separate weaning animals into two groups based on prey size and composition. The analysis finds the best split of specimens that maximizes between-group variance while minimizing within-group variance by iteratively splitting groups and reassigning individuals. We examined the length distributions of specimens from both groups to determine if the technique had identified a meaningful breakpoint in the size or type of prey taken.

Results

Of the 203 stomachs examined, seven contained only milk, and seven contained milk and solid food. The remaining 189 stomachs contained solid food only. The smallest specimen with solid food in its stomach was 115 cm long, and the largest with milk was 160 cm. Of the 29 that were aged, six had milk, five had milk and solid food, and 18 had solid food only. The youngest with solid food in its stomach was 0.5 yr old, while the oldest with milk was 1.8 yr old.

Stomach fullness indices (SFI) ranged from 0.4 to 86.4. There was a significant relationship between length of chase and SFI (ANOVA $F = 1.59$, df = 5, $P = 0.17$).

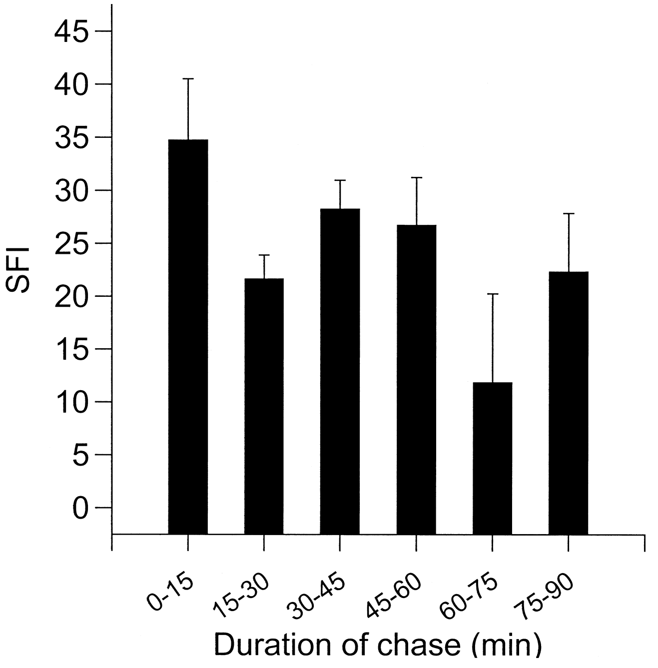

Figure 2. Least squares means of stomach fullness index (SFI) after ANCOVA adjustment for time of day. Duration of chase binned into 15-min increments. Bars represent standard error of mean.

However, when time of day was used as a covariate, the adjusted means of SFI were significantly different among chase length bins (ANOVA $F = 2.28$, df $= 5$, $P = 0.048$, Fig. 2). This indicates that animals experiencing longer chases are likely to have emptier stomachs. There was no significant difference between length of chase and the mean body length of specimens examined (ANOVA $F = 1.07$, df $= 5$, $P = 0.38$).

Weaning Models

The estimated logistic models (Fig. 3) for weaning relative to length were

$$p(milk) = \frac{1}{1 + e^{-13.48+0.11length}},$$
$$p(food) = \frac{1}{1 + e^{26.67-0.24length}}.$$

The length at which $p(milk) = 0.5$ was 122 cm (95%CI = 112–130 cm). The length at the same probability for $p(food)$ was 113 cm (95%CI = 103–121 cm). The two curves intersected at a probability of 0.66 and a length of 116 cm.

The estimated models of the relationship of $p(milk)$ and $p(food)$ relative to age (Fig. 4) were

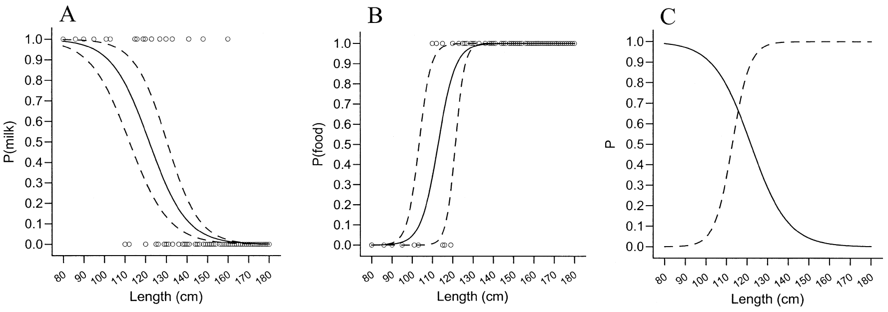

Figure 3. Logistic models for (A) *p(milk)*, and (B) *P(food)* relative to body length (n = 203 stomachs). Dashed lines in graphs A and B represent 95%CI from 5,000 bootstraps. Graph C shows overlay of *p(milk)* (solid line) and *p(food)* (dashed line). Model parameters given in text.

$$p(milk) = \frac{1}{1 + e^{-1.95+2.53age}},$$
$$p(food) = \frac{1}{1 + e^{3.87-7.05age}}.$$

From these equations, *p(milk)* = 0.5 at approximately 0.8 yr (95%CI = 0.3–1.3 yr) and *p(food)* = 0.5 at 0.6 yr (95%CI = 0.3–0.8 yr). The probability at which the two curves intersected was 0.60, which corresponds to an age of 0.6 yr.

Prey Habits of Small- and Large-weaners

Based on the model, length at *p(milk)* = 0.01 was 163 cm. The median length of the 84 specimens with solid food in their stomachs less than or equal to this value was 156 cm. Thus, we designated the 40 specimens from 110 to 154 cm as "small-weaners" and the 43 specimens from 156 to 163 cm as "large-weaners" (group sizes not equal because five specimens were 156 cm long). Large-weaners tended to have more prey items (both fish and squid) in their stomachs (Table 1). There was no significant difference in the frequency of occurrence of fish between the two categories (t = −1.57, df = 81, P = 0.12). However, the squid families Ommastrephidae, Onychoteuthidae, and Cranchiidae showed a significant increase of occurrence of approximately 30% in late-weaner stomachs.

Squid beaks from 9 of 16 species could be converted to mantle length (Table 2). It was possible to convert otolith length to body length for only three species of fish. This was mostly due to erosion from digestion and lack of available regression equations. The average prey size was 51.6 mm ± 0.80 and the median was 36.5 mm. Prey sizes were available from 53 stomachs (Fig. 5). There was no significant difference in the size of fish captured by small- or large- weaners (t = 0.37, df = 298, P = 0.71). However, large- weaners were found to take squid which were approximately 11 mm larger on average (t = –5.96, df = 1835, $P < 0.001$).

Because sample sizes were small for otolith regressions, we conducted the k-means clustering using data from squid only. A Principal Components Analysis on the occurrence of the five major squid families identified a second component that was primarily a contrast between the presence of Ommastrephidae (positive loadings) and the presence of Enoploteuthidae and Mastigoteuthidae (negative loadings). This component accounted for 28% of the variance in the data.

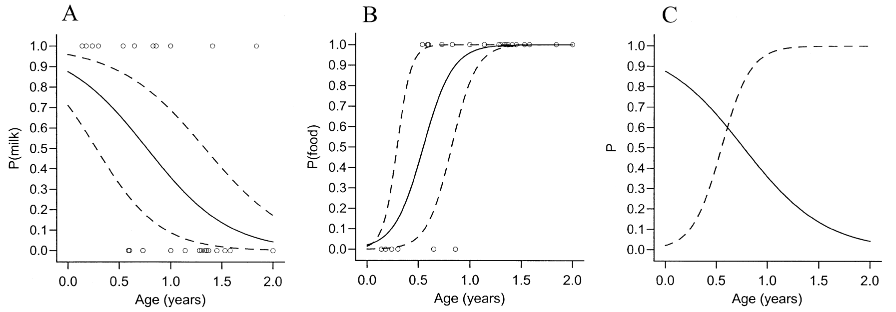

Figure 4. Logistic models for (A) *p(milk)*, and (B) *P(food)* relative to age ($n = 29$ stomachs). Dashed lines in graphs A and B represent 95%CI from 5,000 bootstraps. Graph C shows overlay of *p(milk)* (solid line) and *pP(food)* (dashed line). Model parameters given in text.

Using the scores on this second component and the mean mantle length of squid found in each individual, the clustering algorithm identified the best two clusters (Fig. 6) of the 53 pre-weaning specimens. The mean body length of the first cluster was 148.7 cm with a range of 110–163 cm, and differed significantly from the second cluster which had a mean body length of 157.2 cm with a range of 152–163 cm ($t = -2.96$, df $= 44$, $P = 0.005$). Individuals in the second cluster tended to consume larger squid and Ommastrephids more than Enoploteuthids and Mastigoteuthids.

Discussion

We have developed logistic models that relate the probability of finding milk or food in spotted dolphin (*Stenella attenuata*) stomachs to the length and age of the animal. Several steps are required to translate these results into a model of weaning, which would describe the transition from dependence on the mother to independence. A primary assumption is that the stomach contents we observed reflected the actual weaning status of each specimen. For example, if a stomach contained milk but not solid food, then the implication is that the calf was obtaining all of its nutrition by suckling. However, the absence of solid food does not necessarily mean that an animal is not feeding itself. If it is in the early stages of weaning, it may not be feeding frequently, therefore what little food that is taken may be missed or already digested. The results of our ANCOVA suggest that some stomach contents may be eliminated prior to sampling by regurgitation during the chase. Evidence of prey consumed may also be eliminated by defecation.[2] The likelihood of regurgitation may vary among calves, becoming less prevalent as the calf ages and gains experience with fishing vessels. The result of not observing food in the stomach of an animal that is, in reality, taking solid food is an overestimation of *p(food)* at a given length or age.

[2] Pryor, K., and I. Kang. 1980. Social behavior and school structure in pelagic porpoises (*Stenella attenuata* and *S. longirostris*) during purse seining for tuna. National Oceanographic and Atmospheric Administration Administrative Report LJ-80-11C (unpublished). 86 pp. Available from SWFSC, 8604 La Jolla Shores Dr., La Jolla, CA 92038.

Table 1. Difference in mean prey number and occurrence between small- ($n = 40$) and large- ($n = 43$) weaning calves. "Number" means the total number of prey individuals estimated from beaks and otoliths found, whereas "Occurrence" represents fraction of stomachs in which they occurred. Values in bold indicate significant t-test for "Number" and Kolmogorov-Smirnov test for "Occurrence" at $P \leq 0.05$.

	Number				Occurrence	
	Small-weaners		Large-weaners		Small-weaners	Large-weaners
Prey	Mean (SE)	Median	Mean (SE)	Median	Mean (SE)	Mean (SE)
Fish	49.6 (22.5)	2	103.8 (26)	3	0.63 (0.08)	0.58 (0.08)
Myctophidae	39.8 (17.6)	2	88.9 (23.9)	1	0.60 (0.08)	0.51 (0.08)
Squid	**21.1 (7.9)**	**2.5**	**55.1 (12.6)**	**8**	0.80 (0.06)	0.95 (0.03)
Ommastrephidae	**2.4 (0.9)**	**0**	**8.1 (2.1)**	**3**	**0.43 (0.08)**	**0.70 (0.07)**
Onychotehutidae	**0.6 (0.2)**	**0**	**4.7 (1.4)**	**0**	**0.18 (0.06)**	**0.49 (0.08)**
Enoploteuthidae	10.5 (4.5)	1	24.5 (7.4)	2	0.60 (0.08)	0.72 (0.07)
Mastigoteuthidae	1.6 (0.7)	0	3.2 (1.1)	1	0.30 (0.07)	0.51 (0.08)
Cranchiidae	**1.1 (0.7)**	**0**	**8.3 (2.6)**	**0**	**0.15 (0.06)**	**0.47 (0.08)**

Likewise, the absence of milk does not necessarily indicate that an animal is not still suckling. Because a chemical test for milk was not conducted, small traces could have been present but missed (Best *et al.* 1984). Additionally, if the calf was older and nearing the time of weaning, it may not have suckled recently or in large quantities. Any milk from the last suckling bout may have been digested or obscured by the presence of solid food (Best *et al.* 1984). These biases will produce a model that underestimates *p(milk)* relative to length or age.

In either case, 33 of the 428 specimens originally examined by Robertson and Chivers (1997), measuring from 70 to 215 cm, had empty stomachs. Thus, there is some opportunity for bias. Our models were also affected by the relative lack of very small animals. This is largely an artifact of the fishery sampling reflected in the age distribution of the kill.[3] The effects of this uneven sampling can be seen in the slightly larger bootstrap confidence intervals at very small lengths (Fig. 3).

If one assumes that the average length or age at weaning is the point where the probability of finding milk in a stomach is 0.5, then from our models, we estimate that this occurs at approximately 122 cm or 0.8 yr in spotted dolphins. On the other hand, if weaning is considered to occur at some higher level of independence, such as when an animal has a very low probability of suckling, it may be more appropriate to use a point like *p(milk)* = 0.05 (approximately 148 cm and 1.9 yr, respectively). The difference between these is more than a year, highly significant in any life history model.

Typically, length or age at weaning in cetaceans is calculated either by direct examination of stomach contents, or more frequently, by assuming that in situations where a large number of individuals have been killed at once, as in the ETP tuna purse-seine fishery, lactating mothers and calves are killed together. In

[3] Archer, F., and S. J. Chivers. 2002. Age structure of the northeastern spotted dolphin incidental kill by year for 1971 to 1990 and 1996 to 2000. National Oceanographic and Atmospheric Administration Administrative Report LJ-02-12 (unpublished). 18 pp. Available from SWFSC, 8604 La Jolla Shores Dr., La Jolla, CA 92038.

Table 2. Mean, standard error, and range of squid mantle length calculated using regression equations (Wolff 1982*a*; Clarke 1986*a*; SWFSC, unpublished data). "Number" represents the total number of beak pairs that were measurable, without being broken or worn.

	Small-weaners		Large-weaners	
Prey Species	Number	Mean ± SE (mm) Range	Number	Mean ± SE (mm) Range
Abraliopsis affinis	419	30.08 ± 5.35 18.69–39.45	675	30.42 ± 5.16 21.66–45.38
Ancistrocheirus lesueuri	8	31.82 ± 15.77 15.11–46.44	26	39.94 ± 7.30 15.11–203.13
Eucleoteuthis luminosa	44	82.37 ± 17.90 57.40–132.59	66	97.71 ± 34.84 63.18–190.43
Leachia dislocata	27	116.44 ± 21.56 91.36–174.96	137	129.81 ± 30.59 60.02–185.41
Mastigoteuthis dentata	32	61.09 ± 16.06 25.04–96.60	104	69.58 ± 15.97 20.56–110.01
Megalocranchia spp.	3	44.36 ± 41.91 2.45–86.28	106	121.17 ± 64.05 12.93–253.93
Onychoteuthis banksii	5	57.41 ± 24.28 27.39–93.06	80	64.21 ± 19.66 8.63–130.59
Ommastrephes bartrami	6	115.69 ± 21.03 86.67–150.37	74	118.23 ± 20.43 78.18–180.09
Pholidoteuthis boschmai	9	75.20 ± 15.62 49.22–106.10	17	96.16 ± 23.34 42.88–137.69

this second, or "cow-calf" method, the length of the largest animal matching the number of lactating mothers killed is taken as the maximum length at weaning. Estimates of average age at weaning in delphinids, primarily from this second method, are around 12–20 mo (Perrin and Reilly 1984, Oftedal 1997).

Perrin *et al*. (1976) previously used both methods to estimate length at weaning for spotted dolphins. In the method most comparable to this study, the distribution of lengths from 24 calves with stomachs containing milk only, milk and solid food, and solid food only, resulted in an estimate weaning occurs around 130 cm. However, using the second "cow-calf" method, Perrin *et al*. (1976) estimated length at weaning to be 137 cm.

However, as shown in Archer *et al*. (2001), it is unlikely that lactating mothers are always killed with their calves. If 130 cm is used as length at independence, approximately 82% of the lactating females killed are killed without their calves. Assuming that separation prior to weaning negatively affects calf survival, this "calf deficit" is probably proportional to some calf mortality above and beyond that encountered outside the fishery. As indicated by Perrin and Reilly (1984), this additional mortality would cause length at weaning using the cow-calf matching method to be overestimated. On the other hand, if observers did not detect all lactating females in a set, then length at weaning would be underestimated.

A related value that is often reported is the length of lactation, or the mean length of time a female in the population spends lactating. Literature on reproductive parameters in odontocetes (Perrin and Reilly 1984, Evans 1987, Oftedal 1997) suggests that for small, pelagic delphinids this value is around 18 mo. Detailed studies of bottlenose dolphins (*Tursiops truncatus*) and Atlantic spotted

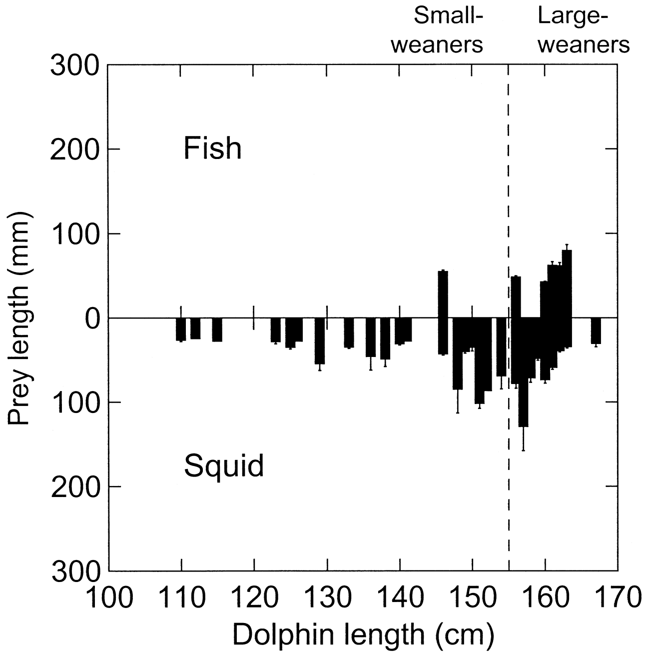

Figure 5. Distribution of mean prey length relative to dolphin length ($n = 53$ stomachs). Mean lengths for fish is on top and squid on bottom. Small-weaners are to left of dashed line (156 cm) and large-weaners to right. Error bars represent one standard deviation.

dolphins (*Stenella frontalis*) show that lactation in some species can last up to 5 yr (Wells 1991, Herzing 1997). If calf mortality is increased above natural rates, length of individual lactation periods would decrease (Perrin and Reilly 1984), although if pregnancy follows quickly upon the death of a young calf, the total percent of time spent lactating could increase. This could happen in the absence of a sharply defined breeding season.

In our comparison of the diets of small- and large-weaners, squid tended to occur more frequently and in larger sizes in the stomachs of larger animals. Fish are higher in caloric content than squid, particularly in fats (Clarke 1986*b*, Croxall and Prince 1982), potentially providing more nutritional value for growth in smaller animals. The increase in prey size with increasing body length of the dolphin has been seen in other studies (Ross 1979, Robertson and Chivers 1997). As the animal grows, it is able to capture and consume larger food. Figure 6 indicates that this happens as a gradual addition of prey to the diet. The increase in the size of squid consumed with increasing body length could be due to the calves' ability to dive deeper as they grow. Adult prey are often found deeper in the water column than juvenile prey (Clarke and Lu 1974, Young 1975). In common dolphins (*Delphinus delphis*) off of South Africa, it was found that the diets of weaning calves were more similar to the diets of non-lactating females than lactating females (Young and Cockcroft 1994) suggesting that these calves are feeding more like average adults.

Inspection of the length distribution and frequency of prey (Fig. 5) suggests that a natural shift in food consumption between small- and large-weaners may occur at a length less than the 156 cm that we used *a-priori* to create our groups. This

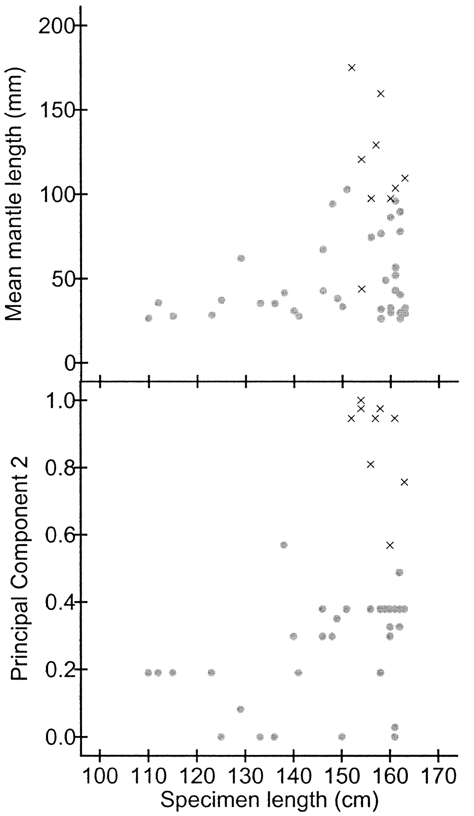

Figure 6. Distribution of mean mantle length and second Principal Component of squid family occurrence relative to specimen length ($n = 53$ stomachs). Crosses and dots represent two clusters designated by *k*-means algorithm.

is confirmed by the results of the *k*-means clustering analysis (Fig. 6), where the smallest animal in the second cluster was 145 cm. This length coincides with a *p(milk)* of 0.07 and represents approximately 2–2.5 yr of age (Hohn and Hammond 1985), again suggesting that true, nutritional independence occurs significantly later in this species than previously reported.

More evidence for this conclusion comes from a study of aerial photographs of the swimming association of mothers and calves of eastern spinner dolphins (*Stenella longirostris orientalis*) in the ETP.[4] The results of this study suggest that spinner calves are swimming independently of their mothers at a length of approximately 142 cm, or 2 yr of age. A previous estimate of the average age at weaning for spinner dolphins from the "cow-calf" method is about a year less (11 mo, Perrin and Reilly 1984), which is similar to previous estimates for spotted dolphins (Perrin

[4] Cramer, K., and W. L. Perryman. 2002. Estimation of reproductive and demographic parameters of the eastern spinner dolphin (*Stenella longirostris orientalis*) using aerial photogrammetry. National Oceanographic and Atmospheric Administration Administrative Report LJ-02-31 (unpublished). 23 pp. Available from SWFSC, 8604 La Jolla Shores Dr., La Jolla, CA 92038.

et al. 1976). This suggests that spinner dolphin calves are also remaining with their mothers well after they are estimated to be nutritionally independent.

In highly social animals such as dolphins, there is probably a significant amount of time between the attainment of nutritional and social independence. At birth, dolphin calves require frequent suckling bouts (Eastcott and Dickinson 1987, Triossi *et al.* 1998), presumably making them vulnerable to extended periods of separation. Suckling may continue as a behavior which reinforces the mother-calf bond (Wells *et al.* 1999). From our model, $p(food) = 0.95$ coincides with $p(milk) = 0.41$, indicating that by the time a majority of calves are taking solid food, they are still suckling at a relatively high frequency. Additionally, in our data, the largest specimen with milk was 160 cm, a length attained between 4 and 6 yr of age (Perrin *et al.* 1976, Hohn and Hammond 1985).

Long life-history tracking studies of bottlenose dolphins (*Tursiops truncatus*) and Atlantic spotted dolphins (*Stenella frontalis*) suggest that suckling by these older calves is likely to be an important biological measure of dependence on the mother (Wells 1991, Herzing, 1997), which, while not nutritionally important, potentially enhances their prospects for survival (Brodie 1969, Smolker *et al.* 1993, Triossi *et al.* 1998). By the time they have weaned and are functionally independent, it is expected that their mortality rates, while still higher than the adult mortality rate, should be decreasing and approaching the mean adult mortality rate.

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